

# A REINTERPRETATION OF ICHTHYOSAUR SWIMMING AND BUOYANCY

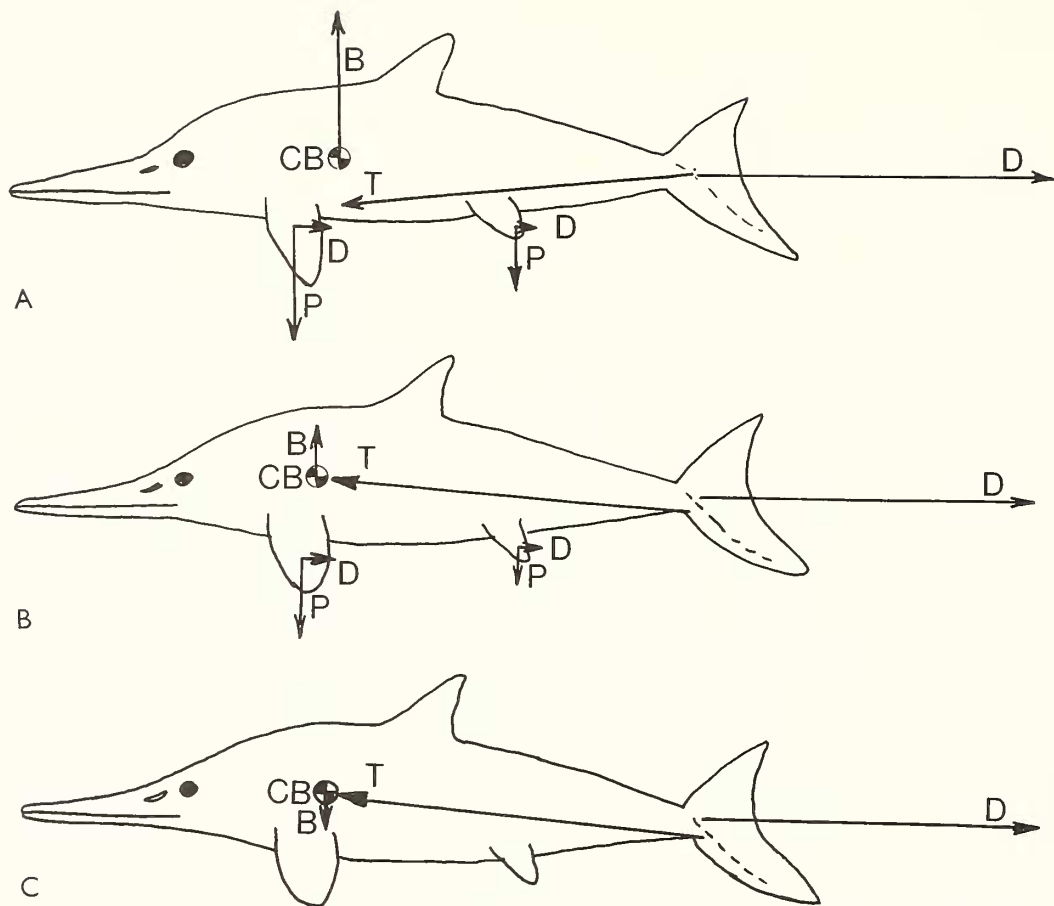
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**ABSTRACT.** A new functional analysis of the reversed heterocercal caudal fin of ichthyosaurs suggests that its function, other than propulsion, was not control of buoyancy, but to produce powerful downwards pitching moments. These moments were used to initiate manoeuvres, to dive after breathing at the surface, and, in one form, to feed. This model is of potential value in analysing the palaeobiology and evolution of ichthyosaurs and other marine reptiles with similar caudal fins.

THE caudal fin of ichthyosaurs is usually assumed to have had the primary function of propelling the animal, but this does not explain why many ichthyosaurs had a caudal fin of the reversed heterocercal type, with a fleshy dorsal lobe, and a ventral lobe containing the terminal vertebral column. Previous studies have inverted existing analyses of the unreversed heterocercal caudal fin of sharks (e.g. Alexander 1974) to conclude that the secondary role of the ichthyosaurian caudal fin was to neutralize positive buoyancy (McGowan 1973). I here apply a new analysis of the shark caudal fin by Thomson (1976) and Thomson and Simanek (1977) to conclude that the secondary role of the ichthyosaurian caudal fin was, rather, to initiate manoeuvres. Furthermore, this new analysis indicates potential new evidence for the palaeobiology of different ichthyosaurs and for the reasons behind the evolution of the reversed heterocercal caudal fin in ichthyosaurs and other marine reptiles.

## FUNCTIONAL ANALYSIS

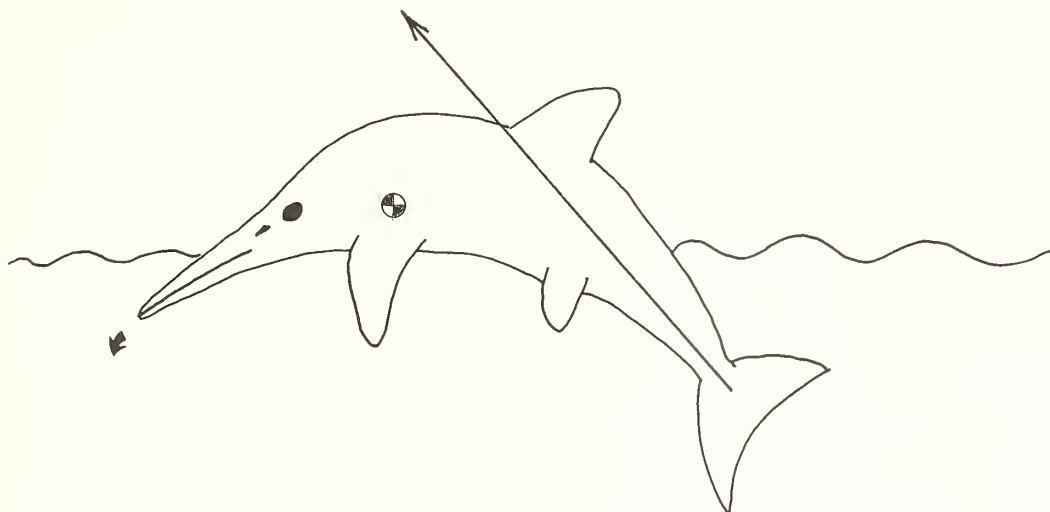
Previous analyses of the swimming and buoyancy of ichthyosaurs (McGowan 1973; Wade 1984) assume that each ichthyosaur was lighter than water and reconstruct the caudal fin as producing a forwards and slightly downwards directed thrust (text-fig. 1A). The downwards component of this thrust has the function of neutralizing part of the upthrust from the negative buoyancy; the remainder of this upthrust is neutralized by lift forces produced by the pectoral fins. The pectoral fins are assumed to be anterior to the centre of balance so that the moment which they produce about the centre of balance is in the opposite sense to, and therefore balances, that produced by the caudal fin. However, by inversion, this analysis is subject to some of the criticisms directed at the original analysis of the shark caudal fin (Alexander 1974; Thomson 1976; Thomson and Simanek 1977). The lift and drag forces vary with speed while the weight and buoyancy remain constant, leading to shifts in the overall balance of forces. In many sharks, and possibly in ichthyosaurs, the pectoral fins are so close to the centre of balance that they have disproportionately short lever arms about the centre of balance and so have to produce large lift and correspondingly large drag forces to counter the moment produced by the caudal fin, with its much longer lever arm (although this could have been alleviated by the use of the pelvic fins). Most importantly, ichthyosaurs were not necessarily lighter than water, and their buoyancy varied with factors such as fatness, repletion or starvation, pregnancy, and above all, the depth of water above the immersed animal (Wade 1984). During a dive, the increase of pressure with depth would compress the air in the lungs and lead to rapid increases in overall density and loss of positive buoyancy and gain of negative buoyancy, as in modern reptiles (Seymour 1982). The ichthyosaur would have had to cope with rapid changes in the magnitude and polarity of its buoyancy.



TEXT-FIG. 1. Old and new models of forces acting on a swimming ichthyosaur. B, upthrust or downthrust due to buoyancy; CB, centre of balance; D, drag; P, hydrodynamic downthrust from pectoral and perhaps pelvic fins; T, propulsive thrust from caudal fin. A, old model, assuming positive buoyancy. The caudal fin's thrust is directed forwards and downwards and has the role of partially counteracting the positive buoyancy. The lift from the pectoral fins counteracts the remaining buoyancy and its moment about the centre of balance counters that from the caudal fin. B, new model, showing how the caudal fin's thrust is forwardly and upwardly directed so as to pass close to or through the centre of balance in normal swimming. The lift from the pectoral (and perhaps pelvic) fins serves only to neutralize upwards or downwards forces remaining from the addition of the upwards component of the caudal fin's thrust to any positive or negative buoyancy. This is the worst case, when the animal is at the surface and positive buoyancy is greatest, and the pectoral and pelvic fins produce lift and therefore drag. C, new model, when the animal has dived to just below neutral depth and it has slight negative buoyancy. The upwards component of the caudal fin's thrust cancels out the negative buoyancy, and the pectoral and pelvic fins need to produce no lift. This is the most efficient situation. Hunting or cruising ichthyosaurs would probably swim in this efficient manner.

The new analysis of the shark caudal fin by Thomson (1976) and Thomson and Simanek (1977) can be inverted to reinterpret the ichthyosaurian caudal fin (text-fig. 1B). The propulsive force from the caudal fin is directed forwards and slightly upwards. Its angle with the horizontal can be varied by controlling the beat of the dorsal and ventral lobes, as in sharks. In an ichthyosaur swimming straight and level, the line of thrust passes through the centre of balance, and the pectoral fins need

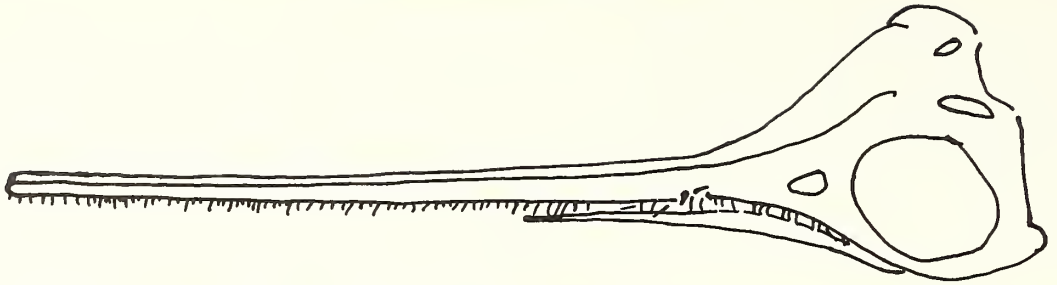
produce only enough lift to compensate for residual up- or down-thrust remaining when the tail's downthrust is added to any positive or negative buoyancy. The lines of thrust from the caudal and pectoral fins pass through, or close to, the centre of balance, so that little or no moments are produced about it and correspondingly little lift and drag are wasted on balancing these moments. The ichthyosaur can now control its buoyancy of whatever magnitude or direction.



TEXT-FIG. 2. The use of the caudal fin in manœuvre. The line of action of the caudal fin can be raised above the centre of balance by modifying the beating of the tail or by flexing the body or both. This produces a strong downwards pitching action which can be used (as here) when starting diving during breathing at the surface, or can be turned into any other manœuvre by use of the pectoral and pelvic fins.

The secondary role of the caudal fin is in manœuvring, as in sharks (Thomson 1976; Thomson and Simanek 1977). The ichthyosaur would initiate a turn by raising the line of thrust of the tail above the centre of balance, producing a strong downwards pitching moment which could be converted by the pectoral and pelvic fins into a turn in any required direction (text-fig. 2). Flexion of the body and tail would contribute to this pitching effect (Appleby 1979). In sharks the positively heterocercal caudal fin produces an upwards pitching action which brings the ventrally located but protrusible mouth into action against prey. By contrast, ichthyosaurs had terminally located narrow rostra. The inverted heterocercal caudal fin would, however, have allowed these air-breathing animals to breathe at the surface. Swimming at, or just below, the water surface is energetically costly because of drag caused by surface turbulence and the production of bow waves (Goldspink 1977). The ichthyosaur could swim up to the surface, start pitching downwards at the surface, and already be diving while it breathed through the nostrils placed high on the sides of the snout just in front of the eyes (text-fig. 2). A strong diving action is particularly important since the animal is most buoyant at the surface.

On the face of it the new analysis of ichthyosaur swimming incorporates an apparent inefficiency (text-fig. 1B). Any positive buoyancy adds to the upwards component of the caudal fin thrust to produce an upthrust which must be neutralized by the production of lift, and therefore drag, by the pectoral and pelvic fins. However, this would be worst at the surface or at shallow depths, when swimming is in any case energetically costly. When the animal dived again, and especially if it exhaled, it would reach neutral depth and then, below that, a point where it became slightly negatively buoyant. At this point the buoyancy and the upthrust from the caudal fin would balance and there



TEXT-FIG. 3. The head of *Eurhinosaurus* showing the greatly undershot lower jaw (after McGowan 1979, pl. 5, fig. 2). Original c. 110 cm long.

would be no need for the pectoral and pelvic fins to produce any lift, and associated drag (text-fig. 1c). The relative magnitude of the upwards component of the caudal fin thrust would depend upon the trade-off between efficient swimming and manoeuvrability, as has been suggested for sharks (Thomson 1976; Thomson and Simanek 1977). A relatively small upwards component, and thus a nearly horizontal line of thrust, would promote minimal drag and therefore high speed, or efficient cruising; a more sharply inclined line of thrust would produce greater manoeuvrability at the expense of efficiency.

#### PALAEOBIOLOGICAL INFERENCES

The aberrant ichthyosaur *Eurhinosaurus* may provide evidence for this hypothesis. It had a long, tooth-armed upper jaw overhanging a much shorter lower jaw (text-fig. 3), and is reconstructed as having slashed downwards through shoals of small fish and cephalopods (McGowan 1979). The ability to pitch downwards strongly is implied by this habit.

Further testing of the hypothesis may come from analysis of variation within ichthyosaurs. In sharks the variation of the caudal fin, especially in the degree of asymmetry about the horizontal axis, the angle of the terminal vertebral column with the horizontal, and the aspect ratio, has been correlated with the ecology of different forms, as this variation controls the angle with the horizontal made by the caudal fin thrust and therefore the balance between manoeuvrability and the energetic efficiency in terms of drag (Thomson 1976; Thomson and Simanek 1977). The existence of exceptional cases of soft part preservation of ichthyosaurs (McGowan 1973, 1979; Martin *et al.*, 1986) provides evidence for the outline of the caudal fin (so long as it is authentic, Riess 1985). This is an opportunity to correlate palaeobiological inferences from caudal fin form with independent evidence from overall body form, paired fin structure, and feeding adaptations, so as to reconstruct the palaeobiology of different ichthyosaurs and different age-classes within species, and test the present hypothesis of caudal fin function.

The hypothesis of caudal fin function will also be relevant to studies of the origin and evolution of the ichthyosaurian reversed heterocercal caudal fin during evolution from terrestrial ancestors, and of the independently evolved reversed heterocercal caudal fin of other marine reptiles such as the thalattosuchian crocodylians (Buffetaut 1979).

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